BOTANY.—Setaria: *Fascicle organization in four species.*[1] ERNEST R. SOHNS, U. S. National Museum. (Communicated by Jason R. Swallen.)

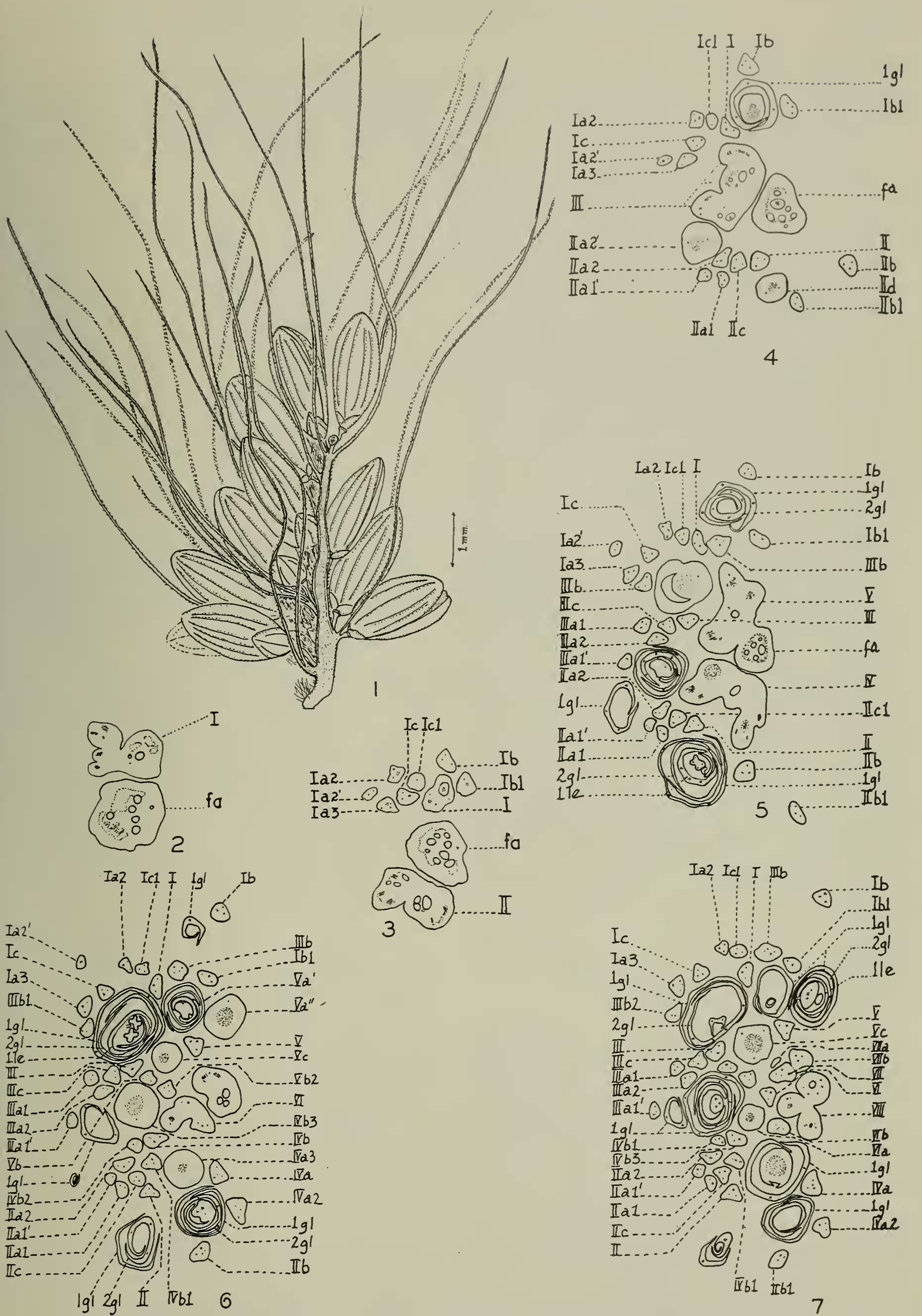
Setaria, a genus of grasses of 100 or more species, is widely distributed in the tropics, subtropics, and temperate regions of the world. Several species are cultivated for ornament; one species (*S. italica*) has been cultivated for food for many centuries and some annual species, especially in the temperate regions of the world, are serious weeds (Bews, 1929; Hitchcock, 1936; Pilger, 1940). Nine species are native in the United States and 13 species have been introduced, 4 of which are cultivated as forage or ornamental grasses (Hitchcock, 1951).

The inflorescence of the species varies from densely spikelike and many-flowered to open and few-flowered. The inflorescence, which is a terminal panicle, is composed of numerous fascicles. Each fascicle contains one or more spikelets and from one to numerous sterile branches (bristles). The sterile branches are persistent on the axis of the fascicle. The fascicle varies in complexity from that of *S. italica*, in which there are numerous spikelets and sterile branches to that of *S. palmifolia* in which there is a spikelet and, occasionally, a single bristle.

The fascicles of several species of *Setaria* have been studied for bristle formation, for the presence or absence of an axis terminus and for the determination of sterile and fertile axes. This study, involving four species of *Setaria*, is concerned with the organization and interpretation of the fascicle as the basic unit of the inflorescence.

Historical.—Goebel (1884), who investigated bristle formation in *S. glauca* and *S. italica*, found that the tip of the inflorescence axis was sterile and prolonged as a bristle. Branching of the fascicle was interpreted as dorsiventral and two-ranked. Only the axes of the second order produced spikelets; the others remained sterile (bristles). Goebel diagrammed the branching of the fascicle in *S. viridis* (see his figure 18). The relationship of first-order branches is not clear, and there is no indication of fertile axes in the diagram. Goebel used entire young fascicles and based his observations on macroscopic examination. He failed to find support for Hofmeister's contention that spikelet formation was initiated on some bristles only later to cease development and fall off. Goebel found the spikelets of *S. italica* and *S. glauca* to contain two florets; the lower staminate or aborted and the upper hermaphrodite. The upper floret, according to Goebel, originated near the axis terminus. The designation of the axis terminus in his drawings (see his figures 11 and 12) is, as Schumann (1890) pointed out, undoubtedly a misinterpretation. Goebel stated that the florets (Blüthe) appear to develop in a terminal position. He observed that the bristles are persistent; that their numbers are variable and that their presence helps prevent the birds from picking the seeds out of the spikelets. Goebel also examined *Pennisetum verticillatum* R. Br. (= *Setaria verticillata* (L.) Beauv.) and concluded that the fascicle of this species was a perfected fascicle of *Setaria*. *S. italica* and *S. glauca* were studied by Schuster (1910). He reviewed the work of Goebel and Schumann and asserted that he found an axis terminus in the upper floret (. . . in der oberen Blüthe einen deutlichen Achsenhöcker hatten . . .) of both species. *Pennisetum verticillatum* R. Br. (= *Setaria verticillata* (L.) Beauv.) was found to have no axis terminus and he agreed with Goebel that "only the ends of axes of second order were fertile, while the bristle-involucre was formed from the remaining sterile lateral branches." Arber (1931) showed that the fascicles of *S. glauca* usually have one spikelet, the lower floret of which is aborted and the upper is perfect. She regards the median spikelet as terminating the axis of the fascicle. It is concluded that "each ultimate-shoot—not each individual bristle—is equivalent to a spikelet." The bristles may be interpreted either as leaf or stem structures; however, it is concluded that the bristles are to be regarded as stems because they "play the part of axes in relation to lateral members; and also because the axis of an abortive

[1] Based on part of a thesis, "The Floral Morphology of *Cenchrus*, *Pennisetum*, *Setaria*, and *Ixophorus*," submitted to the faculty of the Graduate School of Indiana University in partial fulfillment of the requirements for the degree doctor of philosophy. The writer is grateful to Dr. Paul Weatherwax for suggesting the problem and for helpful suggestions throughout the investigation.



FIGS. 1–7.—1, Typical fascicle of *Setaria italica* (Farwell 5607a, Oxford, Mich.); 2–7, diagrammatic transsections of a fascicle of *S. italica*. (*fa*—fascicle axis; *1 gl*—first glume; *2 gl*—second glume; *1 le*—lemma of the lower floret; *2 le*—lemma of the upper floret; *I*, *II*, *III*, etc.—first-order branch; *a*, *b*, *c*, etc.—second-order branch; *a* 1, *b* 1, *c* 1, etc.—third-order branch; *a* 1′, *b* 1′, *c* 1′, etc.—fourth-order branch; *a′* and *a″*—two branches of equal rank. All figures approximately ×25.)

spikelet may be bristle like . . . ." She does not agree with Goebel's interpretation of the branching of the fascicle. These views were reaffirmed in her studies in 1934.

Materials and Methods.—Dr. Paul Weatherwax provided seeds of *S. italica* and *S. palmifolia*. *S. glauca* and *S. viridis* were collected in Indiana by the writer. Specimens were deposited in the Herbarium of Indiana University. Fascicles were collected and processed by standard methods in microtechnique.

Discussion.—A fascicle of *S. italica* is shown in Fig. 1. It has a central axis (fascicle axis) and numerous lateral branches. Each lateral branch of the central axis is designated as a branch of the first-order, from which arise lateral members (second-, third-, and fourth-order branches, etc.). Serial sections through a fascicle, from the base upwards, provide a means whereby the branching system of a typical fascicle as well as the relationship of spikelets and bristles may be shown. A selected series of such transsections, taken from a detailed series of drawings prepared by the writer (1949), is shown in Figs. 2–7. Fig. 2, a diagrammatic transsection through the base of the fascicle, shows the fascicle axis (*fa*) and a first-order branch (*I*). Fig. 3, at a higher level, shows the branches produced by first-order branch I, the base of the next higher first-order branch II and the fascicle axis. The following figures (Figs. 4–7) were drawn from serial sections at successively higher levels to show the branching of the fascicle and the relationship of spikelets and bristles. The relationship of the fascicle axis and its lateral members is shown diagrammatically in Fig. 8. A branch of any order may be spikelet-bearing, or a lateral branch and its members may be completely sterile.

The upper floret is readily deciduous at maturity leaving the lower floret and glumes remaining in the fascicle. The abcission of the floret from the spikelet of a Panicoid grass is a relatively rare occurrence. One of the distinguishing features of the Panicoid grasses is abscission of the spikelet below the glumes. The abscission of the fertile floret in *S. italica* unquestionably played an important part in the selection of this species for cultivation and subsequent domestication. The upper floret has lodicules.

A fascicle may contain as many as fifteen spikelets. Apparently only those in the upper part of the fascicle are fertile since the number of caryopses ranged from two to five (*S. italica*).

Most bristles have three vascular bundles and in the terminal portion of the bristles the vascular bundles may have sheaths. Among the epidermal cells of the bristles an occasional stoma may be found.

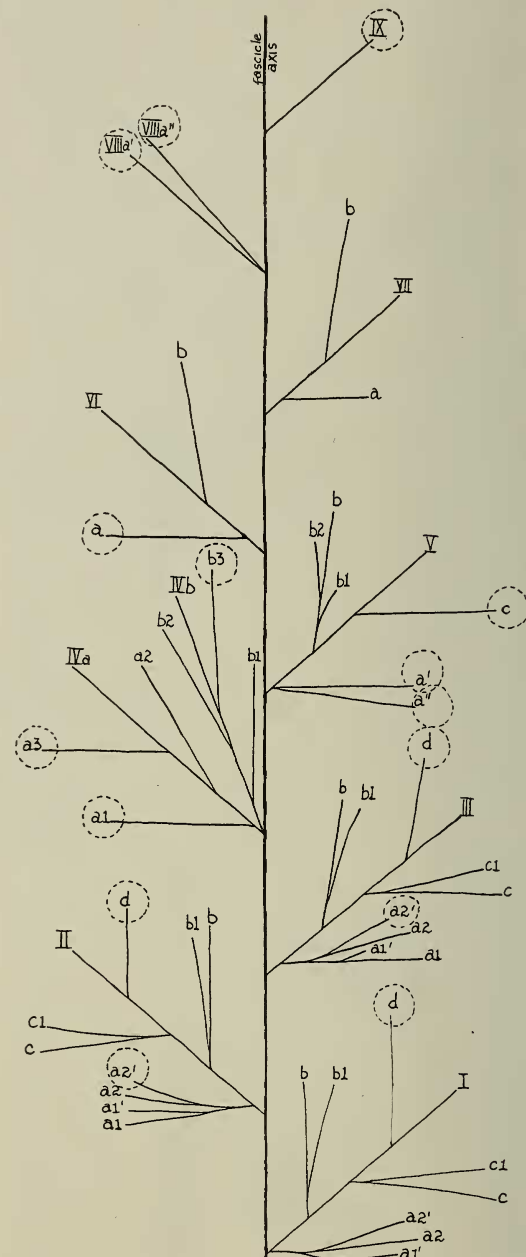


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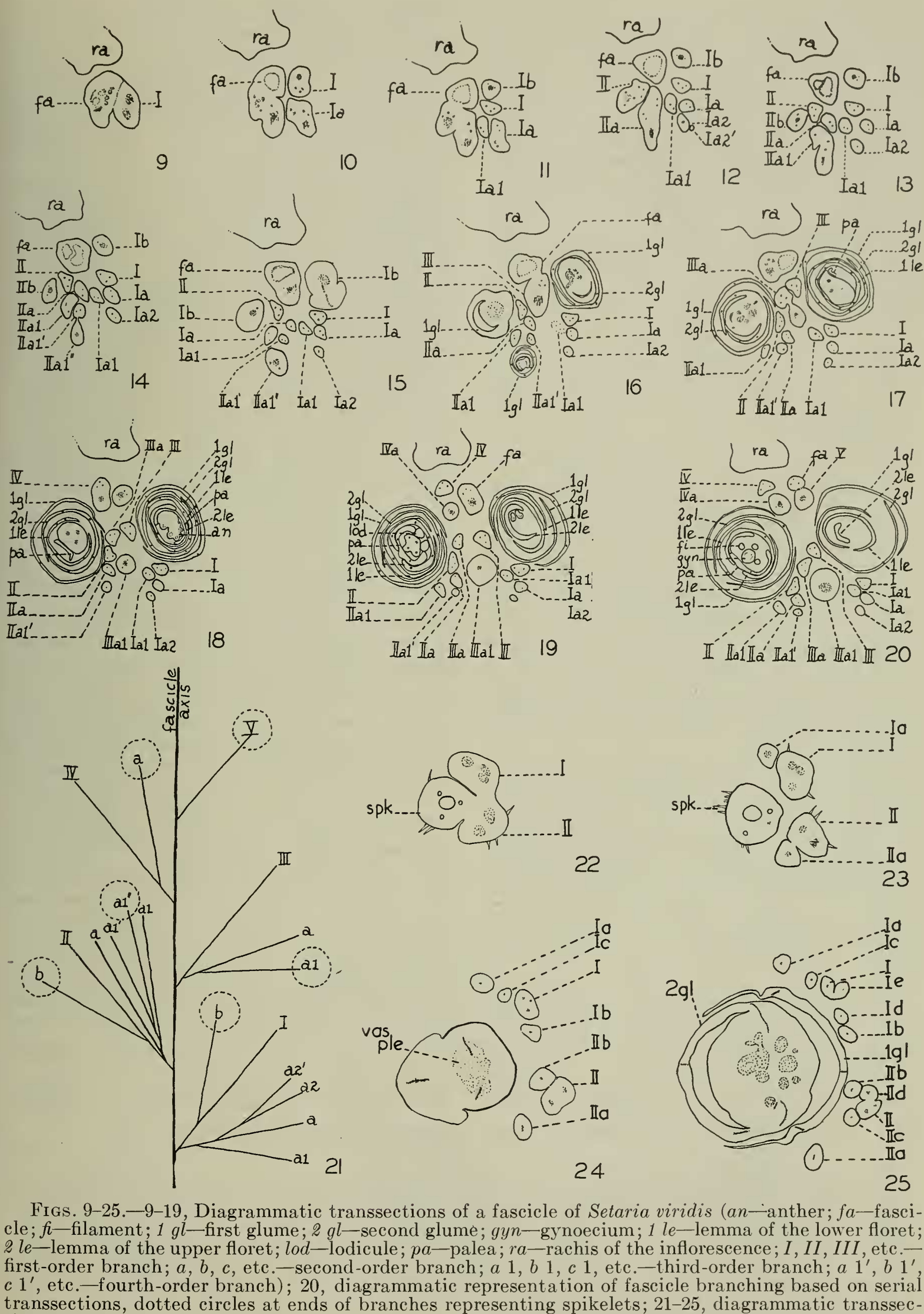
FIG. 8.—Diagrammatic representation of branching in a typical fascicle from the inflorescence of *Setaria italica* as constructed from serial transsections. Dotted circles at ends of branches represent spikelets.



FIGS. 9–25.—9–19, Diagrammatic transsections of a fascicle of *Setaria viridis* (*an*—anther; *fa*—fascicle; *fi*—filament; *1 gl*—first glume; *2 gl*—second glume; *gyn*—gynoecium; *1 le*—lemma of the lower floret; *2 le*—lemma of the upper floret; *lod*—lodicule; *pa*—palea; *ra*—rachis of the inflorescence; *I*, *II*, *III*, etc.—first-order branch; *a*, *b*, *c*, etc.—second-order branch; *a* 1, *b* 1, *c* 1, etc.—third-order branch; *a* 1′, *b* 1′, *c* 1′, etc.—fourth-order branch); 20, diagrammatic representation of fascicle branching based on serial transsections, dotted circles at ends of branches representing spikelets; 21–25, diagrammatic transsections of a fascicle of *Setaria glauca*. (Symbols as above plus *spk*—spikelet; *vas ple*—vascular plexus. All figures approximately ×25.)

Diagrammatic transsections of a fascicle of *S. viridis* (L.) Beauv. are shown in Figs. 9–20. Fig. 9 is a diagrammatic transsection of the rachis (*ra*) of the inflorescence and the base of the fascicle (*fa*) showing a branch of the first-order (*I*). The transsections following are made from serial sections at successively higher levels in the same fascicle. The fascicles are smaller and fewer flowered than those of *S. italica*. Fascicle branching is also like that of *S. italica*, i.e., any order of branch may be spikelet-bearing. The upper florets in this species also have lodicules. A diagrammatic representation of the fascicle and its branches, based on this series of transsections, is shown in Fig. 21. The observations made for the bristles of *S. italica* likewise apply to this species.

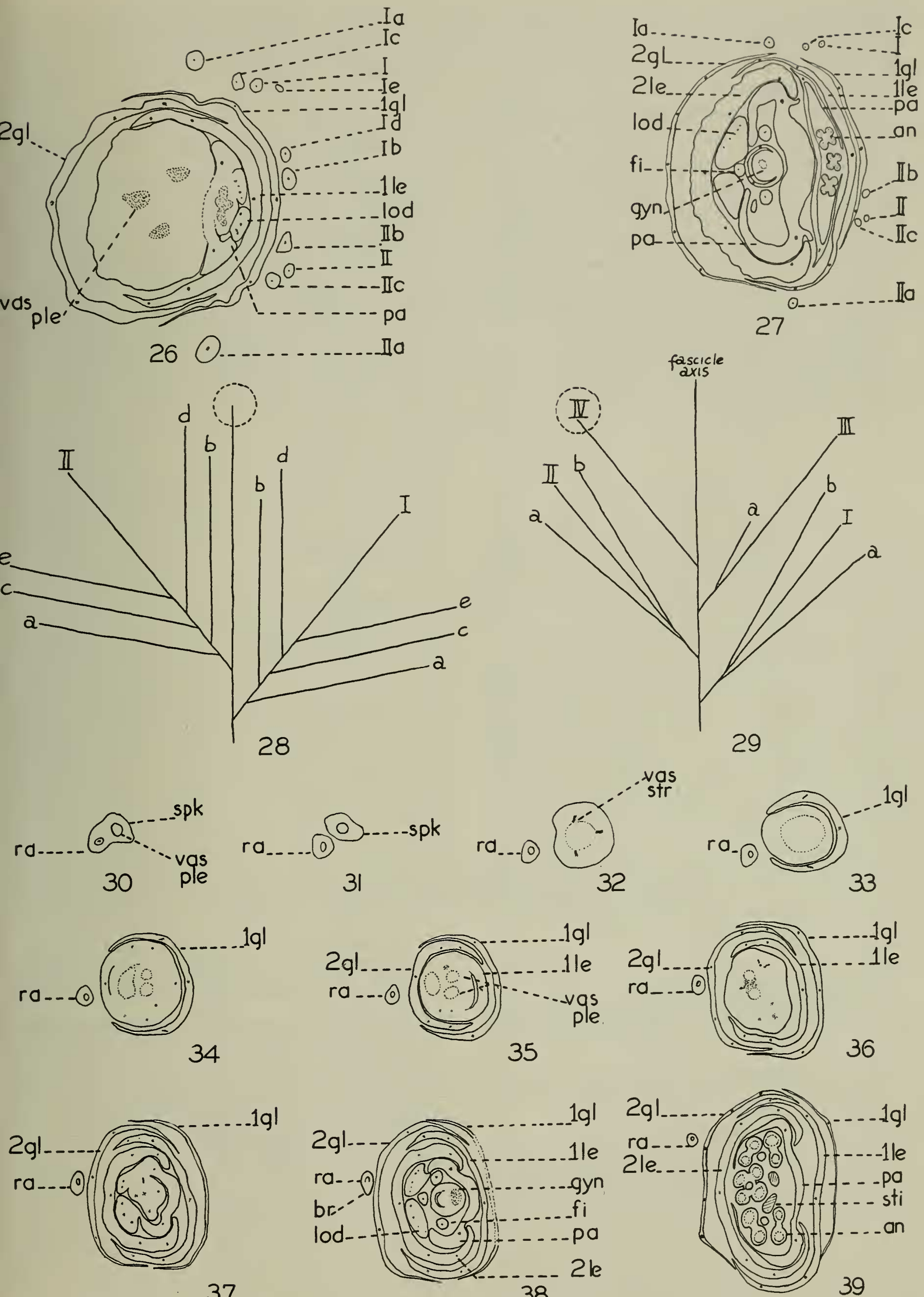
Diagrammatic transsections of a fascicle of *S. glauca* (L.) Beauv. are shown in Figs. 22–27. This fascicle has only one spikelet, but fascicles with two or three spikelets were not uncommon. Branching of the first-order axes is similar to that in *S. italica* and *S. viridis*. Both the upper and lower florets have lodicules. The relationship of the branches within the fascicle is shown diagrammatically in Fig. 28. The fascicle axis, in this example, is terminated by a spikelet. Fig. 29 is a diagrammatic representation of another fascicle from the same inflorescence in which the fascicle axis is sterile.

Most first-order branches, which are triangular in outline, have three vascular bundles. Sheaths may be present around the vascular bundles, especially in the terminal portion of the bristles. Most second- and third-order branches, which are round or only slightly angled, have two vascular bundles. Although the epidermis has a thick layer of cutin, an occasional stoma may be found.

S. palmifolia (Willd.) Stapf has a simple fascicle, as illustrated in Figs. 30–38. A single bristle (the fascicle axis) extends beyond some of the spikelets. Bristles may not be associated with many of the shortly pedicellate spikelets. The tip of a lateral branch, bearing several spikelets or fascicles, is prolonged beyond the terminal spikelet. Branching of the fascicle axis is suppressed, but the beginning of a branch (*br*, Fig. 38) can be detected in some axes. There is a divergence of the vascular strand, but the branch terminates as a slight ridge or bulge. The upper florets have lodicules.

The complexity of the fascicle varies from that shown in *S. italica* to the simple fascicle of *S. palmifolia*. On the basis of this study, each fascicle in the inflorescences of *S. italica*, *S. viridis* and *S. glauca* is to be compared to a miniature panicle. The branching of the individual fascicle appears to be alternate, but the proximity of the fascicle axis to the rachis (as a result of compression) has obscured the arrangement (probably spiral) of the first-order branches. In *S. italica*, the branches of the first-order appear alternately arranged on the fascicle axis, i.e., if one imagines the axis of the fascicle as a circle divided into four quadrants (Fig. 40), then first-order branches II, IV, VI, and VIII arise in quadrant three and first-order branches I, III, V, VII and IX occur in quadrant four. (First-order branch IX is not shown in the figures included in this paper). In complex fascicles, like those of *S. italica* and *S. viridis* there is progressive sterilization from the top to the base, i.e., the lowermost first-order branches have more sterile lateral members than the upper first-order branches. However, branches of any order may be spikelet-bearing. Inflorescences having complex fascicles may be regarded as primitive. The axis terminus, as well as the first- and second-order branches, in *S. glauca* may be fertile. The fascicle of this species is less complicated and may be derived from the type present in *S. italica* and *S. viridis* by a decrease in the length of the fascicle axis and a suppression of the lateral branches. *S. palmifolia*, with its single bristle, suggests relationship to the section *Paurochaetium* of the genus *Panicum*. Every branch of the fascicle in the species of *Setaria* included in this study may be regarded as potentially spikelet-bearing.

FIGS. 26–39.—26–27, Diagrammatic transsection of a fascicle of *Setaria glauca* (*an*—anther; *fi*—filament; *gyn*—gynoecium; *1 gl*—first glume; *2 gl*—second glume; *1 le*—lemma of the lower floret; *2 le*—lemma of the upper floret; *lod*—lodicule; *pa*—palea; *vas ple*—vascular plexus; *I*, *II*—first-order branch; *a*, *b*, etc.—second-order branch. Fig. 26 approximately ×25; Fig. 27 approximately ×18); 28–29, diagrammatic representations of fascicle branching based on serial transsections, dotted circles at ends of branches representing spikelets; 30–39, diagrammatic transsections of fascicle of *S. palmifolia* (abbreviations as for Figs. 26 and 27 plus *br*—rudimentary first-order branch; *ra*—rachis; *spk*—spikelet; *sti*—stigma). (All figures approximately ×25.)



Figs. 26–39.—(See opposite page for legend).

In the Gramineae, among many "primitive" and "advanced" features, it is generally considered that evolutionary "advance" is from many-flowered spikelets in clusters to single, one-flowered spikelets and from spikelets which have a prolongation of the spikelet axis to spikelets which have one or two florets, one of these terminating the spikelet axis. These criteria appear to apply to these species of *Setaria*, i.e., complicated, complex fascicles consisting of many spikelets and bristles are interpreted as more primitive than fascicles in which the lateral branches are suppressed and the single spikelet, with two florets, terminates the axis.

Summary.—This study, based on four species of *Setaria* (*S. italica*, *S. viridis*, *S. glauca* and *S. palmifolia*), is concerned with the organization of the fascicle. The fascicles of *S. italica* and *S. viridis* are complex, with several first-order branches; they differ from each other only in number of spikelets and bristles. *S. glauca* has a less complicated fascicle, usually with two first-order branches, one or two spikelets, either produced on the fascicle axis or on lateral branches, and *S. palmifolia* has a single bristle (the fascicle axis) extending beyond some, but not all, of the spikelets. Branching of complex fascicles appears to be alternate. Each bristle is considered potentially spikelet-bearing. The upper florets in all species have lodicules and *S. glauca* has lodicules in both florets.

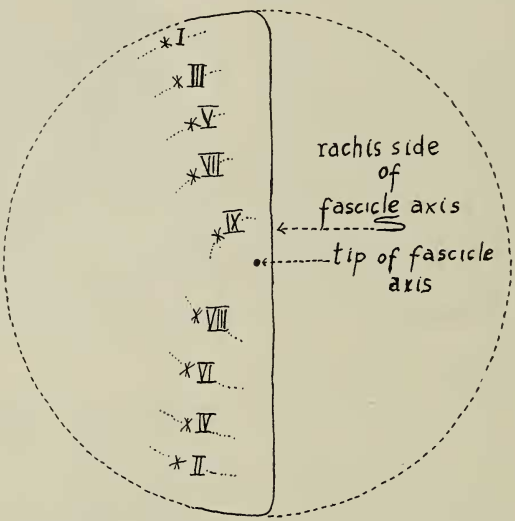


Fig. 40.—Diagrammatic representation of the fascicle axis of *S. italica*. First-order branches I–IX (from the base upward) are indicated by asterisks.

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